LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *UROPHORA TIMBERLAKEI* BLANC AND FOOTE (DIPTERA: TEPHRITIDAE) ON NATIVE ASTERACEAE IN SOUTHERN CALIFORNIA

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Abstract.—*Urophora timberlakei* Blanc and Foote is a bivoltine, probably trivoltine, tephritid which develops in the flower heads of *Acamptopappus, Amphipappus, Chryso-thamnus,* and *Haplopappus* spp. in southern California. For the first time, the egg, second and third instar larvae, and puparium are described, and the larvae and puparium are figured. Distinctive morphological features noted for the immature stages include eggs that are smaller and of a shape different from Palearctic *Urophora.* The third instars resemble certain described Palearctic *Urophora,* but they differ from larvae of other Ne-arctic tephritids in having a bluntly truncated, dark brown to black caudal segment covered by minute dome-shaped papillae and bearing several deep pits mediad and ventrad of the posterior spiracular plates. The verruciform sensilla circumscribing the prothorax and the wedge-shaped acanthae that circumscribe the meso-, metathoracic, and abdominal seg-ments also are distinctive features. The larvae feed mainly on the ovules and soft achenes. Pupariation occurs in the larval feeding chamber among fragments of achenes. Premating and mating behaviors are described for the first time for any Nearctic *Urophora,* distin-guished only by the males displaying abdominal pleural distensions throughout courtship and copulation. *Eupelmus* sp. (Hymenoptera: Eupelmidae) is reported as a solitary, en-doparasitic, larval-pupal or pupal parasitoid.

Key Words: Insecta, *Urophora timberlakei,* nonfrugivorous Tephritidae, mating behav-ior, immature stages, Asteraceae, flower-head feeding

The genus *Urophora* (Diptera: Tephriti-dae) is a polyphyletic assemblage of flori-vorous and/or gallicolous species of fruit flies best known from the Palearctic Re-gion, where several species infesting knap-weeds and thistles [Asteraceae: Cynareae (Centarinae and Carduinae, respectively)] were extensively studied and subsequently exported to North America for biological control of weeds (Varley 1937, Zwölfer 1988, Harris 1989, Julien 1992). Known species of New World *Urophora* were de-picted in a pictorial key by Steyskal (1979), and those found North of Mexico, including eight introduced Old World species, were reviewed and distinguished by Foote et al. (1993). Little is known about the biologies of the eight indigenous North American species of *Urophora* (Foote et al. 1993); however, all seven California species are non-gallicolous, seed-feeders in flower heads of hosts in the subtribe Solidagininae of the tribe Astereae (Asteraceae) (Goeden 1987, unpublished data).

This paper describes the life history and immature stages of *Urophora timberlakei* Blanc and Foote, the first North American species of *Urophora* to be studied in any detail.

Materials and Methods

This study began in 1989 and was based in part on dissections of selected subsamples of mature flower heads of Asteraceae infested by *U. timberlakei* from among many samples collected annually throughout California in the manner described by Goeden (1985, 1987, 1992). Adults studied were reared in wooden, $35 \times 32 \times 35$-cm, muslin cloth-backed, glass-topped sleeve cages in the insectary of the Department of Entomology, University of California, Riverside, from 1-liter samples of mature flower heads at 14-h photophase and $27 \pm 1°C$. Additional adults and parasitoids were reared from larvae and puparia of *U. timberlakei* dissected from flower heads and held separately in cotton-stoppered glass shell vials within humidty chambers in the laboratory at $23 \pm 2°C$ and 76% R.H. All larvae and five puparia dissected from flower head samples were fixed in 70% EtOH for scanning electron microscopy (SEM). Specimens for SEM later were rehydrated to distilled water in a decreasing series of acidulated EtOH, rinsed in hexanes, and post-fixed in 2% aqueous osmium tetroxide for 24 h. They were then dehydrated through an increasing series of acidulated EtOH, critical-point dried, mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a JEOL JSM C-35 scanning electron microscope in the Department of Nematology, University of California, Riverside. SEM micrographs were prepared on Polaroid® P/N 55 film at 15 kV accelerating voltage.

Most adults reared from isolated puparia, as well as overwintered adults swept from preblossom and early-blossom *Acamptopappus sphaerocephalus* (Harvey and Gray) Gray 1 km N of Snow Creek Village, San Gorgonio River flood plain, 350m elevation, Riverside Co., in April, 1992-94, were individually caged in 850-ml, clear-plastic, screened-top cages each fitted with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cagings were used for longevity studies and oviposition tests. Virgin male and female flies of known ages obtained from emergence vials were paired in clear-plastic, disposable petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey for direct observations, videorecording, and still-photography of their general behavior, courtship, and copulation (Headrick and Goeden 1991). Three trials with *U. timberlakei* reared from the flower heads of *Chrysothamnus teretifolius* (Durand and Hilgard) Hall were held together for a maximum of 14 days, and observations were made as opportunity allowed throughout each day.

Plant names used in this paper follow Munz and Keck (1959) and Munz (1968, 1974); names for flower head parts follow Hickman (1993). Tephritid names and anatomical terms follow Foote et al. (1993); nomenclature used to describe the immature stages follows Headrick and Goeden (1990, 1991), Goeden and Headrick (1990, 1991a, b; 1992), and the telegraphic format of Goeden et al. (1993, 1994). Means $\pm$ SE are used throughout this paper. Voucher specimens of reared adults of *U. timberlakei* and its parasitoids reside in the research collections of RDG; preserved specimens of larvae and puparia are stored in collections of immature Tephritidae maintained by JAT.

Results and Discussion
Taxonomy

Urophora timberlakei was described by Blanc and Foote (1961). Photographs of the characteristically hyaline wing occurring in both sexes of this species were provided by Foote and Blanc (1963) and Foote et al. (1993). The aculeus of the female was illustrated by Steyskal (1979). The adults of *U. timberlakei* heretofore have not otherwise been illustrated nor the immature stages described or illustrated.

Egg.—Egg body smooth, shiny, white, elongate-ellipsoidal; anterior end tapered,

bearing peg-like, 0.02 mm-long pedicel; posterior end tapered, smoothly rounded. Twenty-one ova dissected from two field-collected females were 0.55 ± 0.004 (range, 0.52–0.58) mm long and 0.15 ± 0.004 (range, 0.12–0.20) mm wide.

Wadsworth (1914) described the ova of *Urophora solstitialis* (L.) as being white, smooth, cresent-shaped, 0.70 mm long and 0.20 mm wide. Persson (1963) described *U. solstitialis* eggs as shiny white, 0.80 mm long, 0.20 mm wide, and having the same shape as those of *U. stylata*. The eggs of *U. timberlakei* are smaller in size and differ in shape from the Palearctic species described above, being more elongate-ellipsoidal than cresent-shaped.

Third instar.—Third instar elongate-cylindrical, tapering slightly anteriorly, bluntly truncated posteriorly (Fig. 1A); integument white, venter of meso-, metathorax with brown infuscation; caudal segment dark brown or black (Fig. 4B, C); minute acanthae circumscribe meso-, metathorax and abdominal segments (Fig. 1A); gnathocephalon conical, smooth, lacking rugose pads (Fig. 1B); paired dorsal sensory organs, dorsomediad of anterior sensory lobe, consist of a single dome-shaped papilla, (Fig. 1C-1, 1D-1); anterior sensory lobes separated by medial depression (Fig. 1C-2), each bearing terminal sensory organ (Fig. 1D-2), pit sensory organ (Fig. 1D-3), lateral sensory organ (Fig. 1D-4), and supralateral sensory organ (Fig. 1D-5); stomal sense organ ventrolaterad of anterior sensory lobe near mouth lumen (Fig. 1C-3, 1D-6); lateral and ventrolateral sensilla verruciform with a central pore (Fig. 1B-1); mouth hooks bidentate, teeth stout, conical (Fig. 1C-4); median oral lobe tapered anteriorly, laterally flattened, attached to labial lobe (Fig. 1C-5); prothorax smooth, minute acanthae anteroventrally (Fig. 1B), verruciform sensilla circumscribe segment, arranged 3-ventral, 3-medial, 2-dorsomedial, 3-dorsolateral (Fig. 1B-2); anterior thoracic spiracles dorsolateral on posterior margin of prothorax each bearing two papillae (Fig. 1B-3,

E); lateral spiracular complex with spiracle (Fig. 1F-1) and two verruciform sensilla on meso- and metathorax, a single verruciform sensillum on abdominal segments (Fig. 1F-2); minute acanthae which circumscribe TII–AVII wedge-shaped with ovoid bases (Fig. 1F-3); caudal segment covered by minute, dome-shaped acanthae (Fig. 1G-1), and numerous deep pits located dorsomediad, mediad and ventrad of posterior spiracular plates (Fig. 1G-2); posterior spiracular plates (Fig. 1G-3, H) distinct, raised, spheroid, bear three oval rimae ca. 0.02 mm in length (Fig. 1H-1), and four, spine-like interspiracular processes ca. 0.006 mm in length (Fig. 1H-2); stelex sensilla surround margin of caudal segment.

Urophora timberlakei larvae fit the general description of other *Urophora* species (Wadsworth 1914, Varley 1937, Persson 1963), and appear closely allied with *U. quadrifasciata*. Both species have anterior spiracles with two papillae, the integument roughened with minute tubercles and the posterior spiracular plates without a pattern of fine grooves or pale border (Varley 1937). *Urophora timberlakei* is different from other Nearctic, non-frugivorous, tephritid species previously examined (Goeden and Headrick 1990, 1991a, b, 1992, Goeden et al. 1993, 1994, Green et al. 1993, Headrick and Goeden 1991, 1993, Novak and Foote 1968, Steck and Wharton 1986) in having a bluntly truncated, dark brown to black caudal segment covered by minute dome-shaped papillae and bearing numerous deep pits dorsomediad, mediad and ventrad of the posterior spiracular plates. The caudal segment of *Euaresta stigmatica* is brown, but smooth and rounded posteriorly (Headrick et al., in press). The posterior spiracular plates appear to be similar to other described species of *Urophora* (Wadsworth 1914, Varley 1937, Persson 1963), but differ from other Tephritidae in being distinctly raised and spheroid in shape (Goeden and Headrick 1990, Goeden et al. 1994, Green et al. 1993, Steck and Wharton 1986). The verruciform sensilla circumscribing the prothorax and the
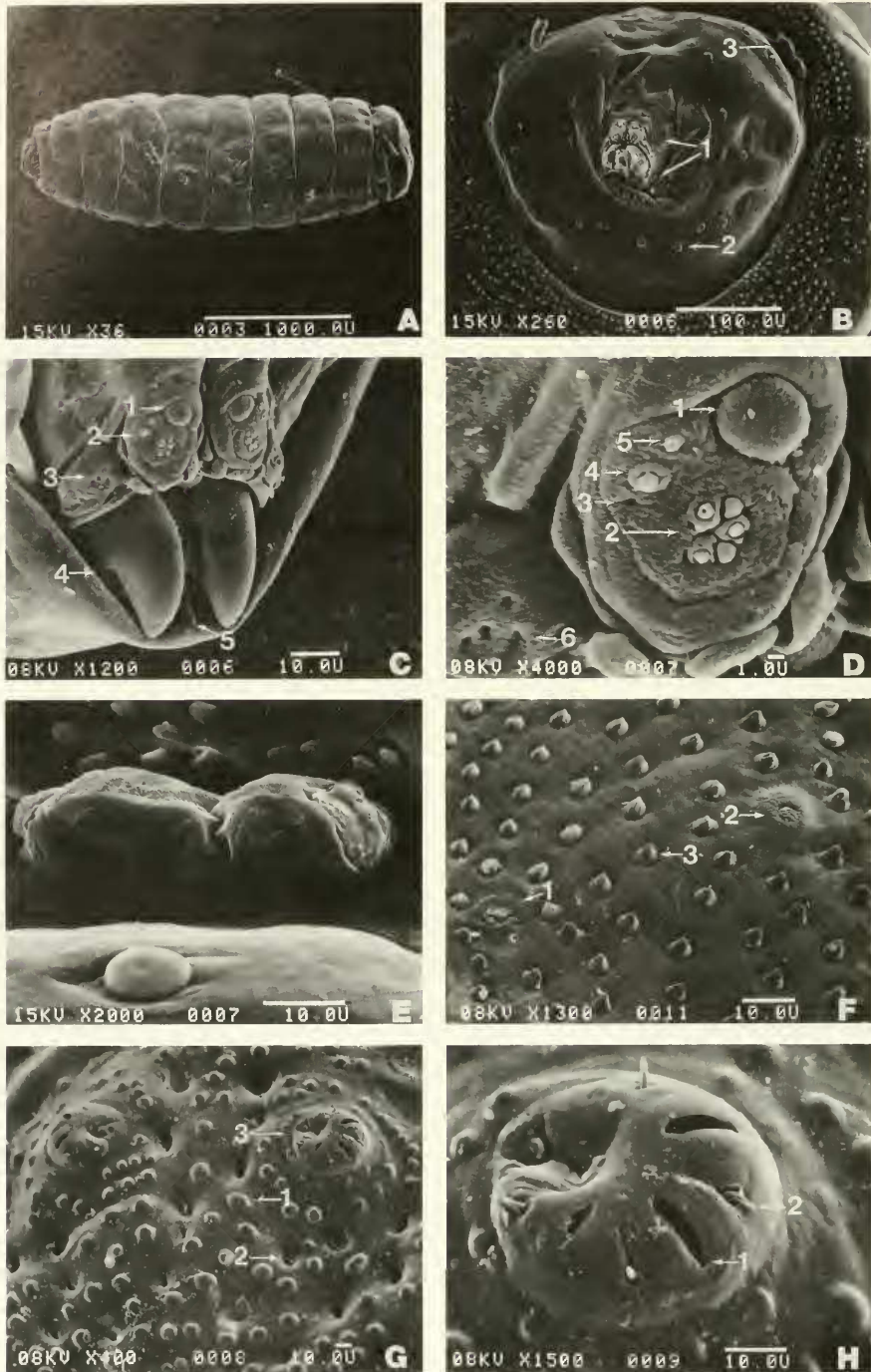
Fig. 1. Third instar larva of *U. timberlakei*: (A) habitus, anterior to left; (B) gnathocephalon, prothorax, anterior view, 1—lateral and ventrolateral sensilla, 2—verruciform sensillum, 3—anterior thoracic spiracle; (C) gnathocephalon, anterior view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—stomal sense organ, 4—mouth hooks, 5—median oral lobe; (D) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—stomal sense organ; (E) anterior thoracic spiracle; (F) lateral spiracular complex, first abdominal segment, 1—spiracle, 2—verruci-

wedge-shaped acanthae which circumscribe the meso-, metathoracic, and abdominal segments are morphological features which may be distinctive of the North American *Urophora*.

Second instar.—Second instar cylindrical, tapered anteriorly, bluntly truncated posteriorly (Fig. 2A); integument white throughout (Fig. 4A); gnathocephalon conical, laterally flattened, smooth, lacking rugose pads (Fig. 2C); paired dorsal sensory organs consist of single round papilla, dorsomediad of anterior sensory lobe (Fig. 2B-1, 2C-1); anterior sensory lobes separated by medial depression (Fig. 2C-2), and bear terminal sensory organ (Fig. 2B-2), pit sensory organ (Fig. 2B-3), lateral sensory organ (Fig. 2B-4) and supralateral sensory organ (Fig. 2B-5); stomal sense organs indistinct, ventrolaterad of anterior sensory lobes, near mouth lumen (Fig. 2B-6, 2C-3); mouth hooks bidentate, teeth sharply curved (Fig. 2C-4); median oral lobe tapered apically, laterally flattened (Fig. 2C-5); small integumental petals dorsad of mouth lumen (Fig. 2C-6); prothorax smooth with minute acanthae ventrad of gnathocephalon; anterior thoracic spiracles consist of two papillae (Fig. 2D); lateral spiracular complex not seen; caudal segment wrinkled with several large depressions mediad of posterior spiracular plates (Fig. 2E); posterior spiracular plates bear three oval rimae ca. 0.007 mm in length (Fig. 2F-1), and four, spine-like interspiracular processes ca. 0.004 mm in length (Fig. 2F-2); stelex sensilla surround margin of caudal segment.

The second instar larva is more cylindrical than the third instar in general body shape. Most morphological features of the second instar are similar in shape and placement to those of the third instar, but not as structurally distinct as on the mature larva. The caudal segment of the second instar larva differs from that of the third instar larva. In the second instar the caudal segment is truncated, white in color, wrinkled and with several large circular depressions. The caudal segment of the second instar lacks the minute dome-shaped acanthae and deep pits mediad and ventrad of the posterior spiracular plates which are present on the third instar. Because of the wrinkled nature of the second instar larvae prepared for SEM, the lateral spiracular complex and the area where prothoracic verruciform sensilla would occur were not observed.

Puparium.—Puparium light brown, anterior end dark brown, caudal segment dark brown to black; elongate cylindrical, tapering anteriorly, truncated posteriorly (Fig. 3A), minute acanthae circumscribe segments (Fig. 3A); anterior end bears the invagination scar (Fig. 3B-1), raised bilobed anterior thoracic spiracles (Fig. 3B-2), and round verruciform prothoracic sensilla (Fig. 3B-3); posterior end comprising of minute dome-shaped acanthae (Fig. 3C-1) and numerous deep pits dorsomediad, mediad and ventrad to the posterior spiracular plates (Fig. 3C-2); posterior spiracular plates bear three oval rimae ca. 0.02 mm in length (Fig. 3D-1), four spine-like interspiracular processes ca. 0.004 mm in length (Fig. 3D-2) and the ecdysial scar (Fig. 3D-3); stelex sensilla surround margin of caudal segment (Fig. 3C-3). Three puparia averaged 2.42 ± 0.62 (range, 2.33–2.54) mm in length and 0.97 ± 0.01 (range, 0.95–0.98) mm in width.

DISTRIBUTION AND HOSTS

The North American distribution of *U. timberlakei* North of Mexico was mapped by Foote et al. (1993) to include California, Colorado, Idaho, Oregon, and Utah, adding Colorado and Utah to the distribution given by Steyskal (1979).

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form sensillum, 3—wedge-shaped acanthae; (G) caudal segment, 1—dome-shaped acanthae, 2—deep pits, 3—posterior spiracular plate; (H) posterior spiracular plate, 1—rima, 2—interspiracular process.
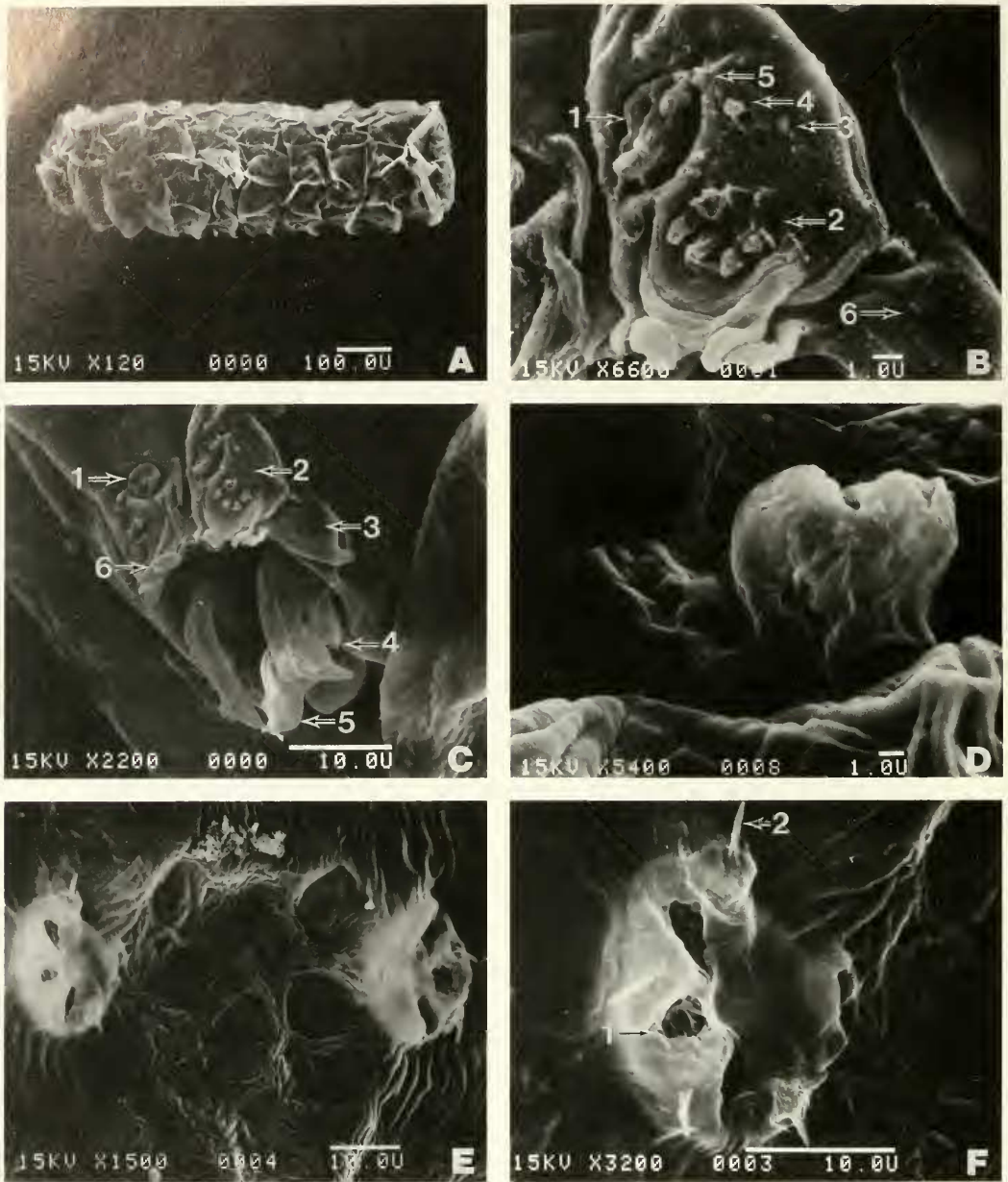
Fig. 2.   Second instar larva of *U. timberlakei*: (A) habitus, anterior to left; (B) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—pit sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—stomal sense organ; (C) gnathocephalon, anterolateral view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—stomal sense organ, 4—mouth hooks, 5—median oral lobe, 6—integumental petals; (D) anterior thoracic spiracle; (E) caudal segment; (F) posterior spiracular plate, 1—rima, 2—interspiracular process.
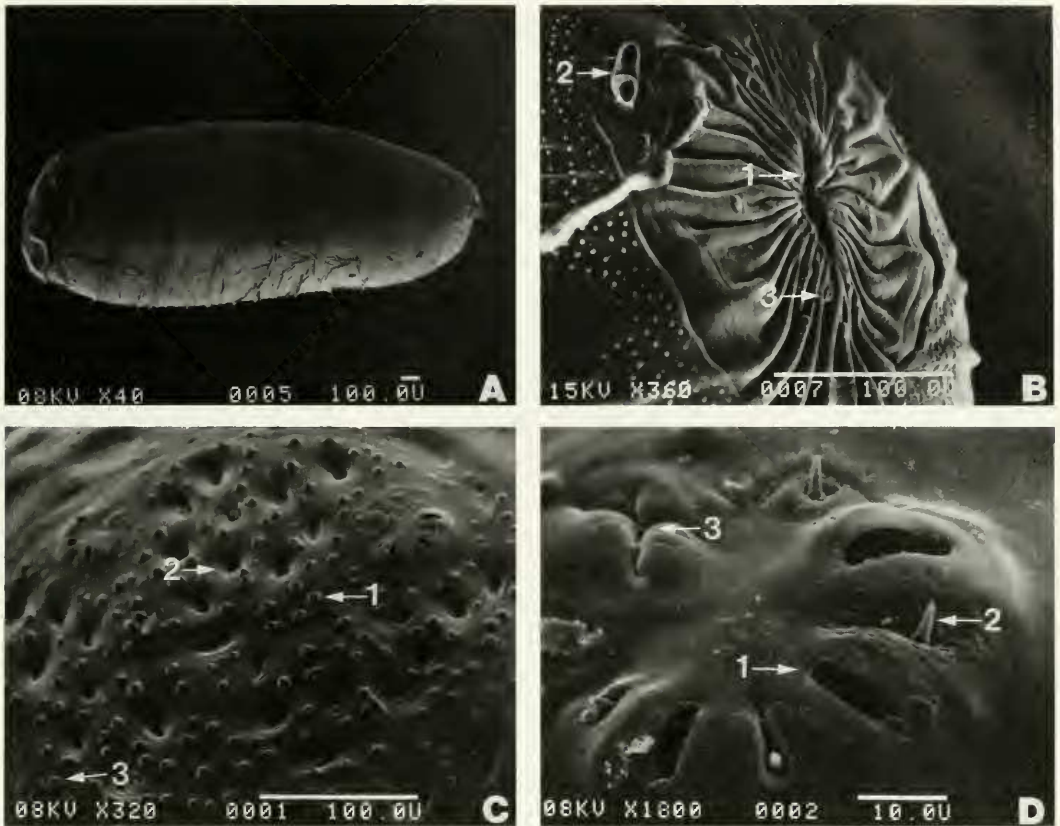
Fig. 3.   Puparium of *U. timberlakei*: (A) habitus, anterior to right; (B) anterior end, 1—invagination scar, 2—anterior thoracic spiracle, 3—verruciform sensillum; (C) caudal segment, 1—dome-shaped acanthae, 2—deep pits, 3—stelex sensillum; (D) posterior spiracular plate, 1—rima, 2—interspiracular process, 3—ecdysial scar.

Goeden (1987) reported this tephritid as reared from flower heads of *Acamptopappus shockleyi* Gray, *A. sphaerocephalus, Chrysothamnus nauseosus* (Pallas) Britton, *C. teretifolius, C. viscidiflorus* (Hooker) Nuttall, *Haplopappus cuneatus* Gray, and *H. laricifolius* Gray. To these confirmed records we add the following new rearing records from ungalled flower heads: *Amphipappus freemontii* Torrey and Gray, 9 ♂ and 7 ♀, W. of Homer Mountain at 884-m elevation, NE San Bernardino Co., 5.v.1988; *C. albidus* (Jones) Greene, 2 ♀, Fish Slough, 9 km N of Bishop at 1,225 m, Inyo Co., 9.x.1990; *C. paniculatus* (Gray) Hall, 1 ♂ and 1 ♀, N of Pioneertown on N rim of Chaparrosa Wash at 1,356 m, SW San Bernardino Co., 31.x.1990; *H. cooperi*

(Gray) Hall, 1 ♂, along Black Canyon Rd., E of Colton Hills, E. Mojave Desert at 1,200 m, NE San Bernardino Co., 30.v.1991.

As first noted by Goeden (1987), and as these new rearing records confirm, the host-plants of *U. timberlakei,* apparently like those of its native congeners in California, all belong to the Subtribe Solidagininae of the Tribe Astereae (Munz and Keck 1959). Most of these new records, like those reported by Goeden (1987), involve only a few flies reared from bulk samples each containing hundreds of flower heads of its mostly small-headed hosts. Like other oligophagous *Urophora* in California, e.g. *U. formosa* (Coquillett), *U. timberlakei* has been reared alone, but more commonly

along with other congeneric or nonconge-
neric species from single samples of host
flower heads (synphagy), sometimes as the
dominant phytophage, but more commonly
subordinate to one or more species of *Neas-
pilota*, *Tephritis*, or *Trupanea* (Goeden
1987, unpublished data). Thus, *U. timber-
lakei* was only occasionally swept, reared,
or otherwise encountered in nature, usually
in synphagy with other species, and there-
fore was not easily studied, even in Cali-
fornia, where it first was described and
since has been reported most frequently
(Foote and Blanc 1963, Foote et al. 1993).

BIOLOGY

Egg.—One of eight (12.5%) infested
heads of *A. shockleyi*, the host with the
largest-sized head in California, and only
one of 61 (2%) infested smaller heads of *C.
teretifolius* and *C. viscidiflorus* examined
during the study period contained two lar-
vae of *U. timberlakei*. Therefore, single
eggs usually are oviposited by individual
females in preblossom heads, but none was
recovered during the present study.

Larva.—All second and third instar lar-
vae observed in dissected heads had con-
fined their feeding to ovules and soft
achenes of individual flower heads (Fig.
4A, B). Larger larvae were found in feeding
cavities located between adjacent achenes
or were confined to individual achenes, and
only partially damaged other ovules as ear-
ly instars. The feeding cavities of *U. tim-
berlakei* always appeared dry, which sug-
gested that sap was not an important sup-
plemental food source for this tephritid, un-
like *Neaspilota viscidiflorus* Quisenberry
(Goeden and Headrick 1992) and several
other, ovule and soft achene-feeding tephri-
tids studied in California to date (Headrick
and Goeden 1990, 1991; Goeden and Head-
rick 1992). In eight (4%) infested heads of
A. shockleyi of 200 examined, third instars
attacked an average of only 1.3 ± 0.2
(range, 1–2) achenes of an average total of
38 ± 1.7 (range, 32–46) achenes, or about
3% of the achenes therein. The receptacle

was slightly scored in only one of these
eight flower heads, which, again, are the
largest among *U. timberlakei's* known hosts
in California. On the other hand, an average
of 3.5 ± 0.4 achenes were damaged and the
receptacles scored in eight, small, infested
heads of *C. viscidiflorus*. Four other sub-
samples of 200 heads each of *C. viscidiflo-
rus* from different locations contained only
0, 2, 3 and 4 (0%, 1%, 1.5%, and 2%, re-
spectively) immature *U. timberlakei*. In a
subsample of 400 heads of another small-
headed host, *C. teretifolius*, 28 (7%) were
infested by *U. timberlakei* larvae that whol-
ly or partly damaged an average of 2.2 ±
0.12 (range, 1–4) ovules and soft achenes
or about half of an average total of 5.0 ±
0.13 (range, 3–6) achenes in each head. The
receptacles were slightly scored in only two
(7%) of these 28 infested heads; whereas,
all four achenes in each of four infested
heads were completely destroyed, and three
of the receptacles scored in a different sub-
sample of 200 heads of *C. teretifolius* from
a different location.

The fully grown third instar (Fig. 4C)
overwinters inside the feeding cavity within
the excavated head which usually remains
attached to the dormant host plant, as with
N. viscidiflorus (Goeden and Headrick
1992), but without forming a hard, protec-
tive cell like the latter species. Among flo-
rivorous, southern California Tephritidae,
only *Urophora*, *Neaspilota*, and possibly
Xenochaeta spp. mainly overwinter within
dead flower heads as nonfeeding, diapaus-
ing, fully grown larvae (Goeden and Head-
rick 1992, Goeden and Teerink, unpub-
lished data); whereas, most other florivo-
rous species emerge in the spring, summer,
or fall and overwinter as adults, e.g., *Neo-
tephritis*, *Paracantha*, *Stenopa*, *Trupanea*,
and *Tephritis* spp., or emerge from heads as
larvae, drop to the ground, and overwinter
as buried puparia, e.g., *Orellia* and many
Paroxyna spp. (Goeden, Teerink, and Head-
rick, unpublished data).

Puparium.—Pupariation occurs in spring
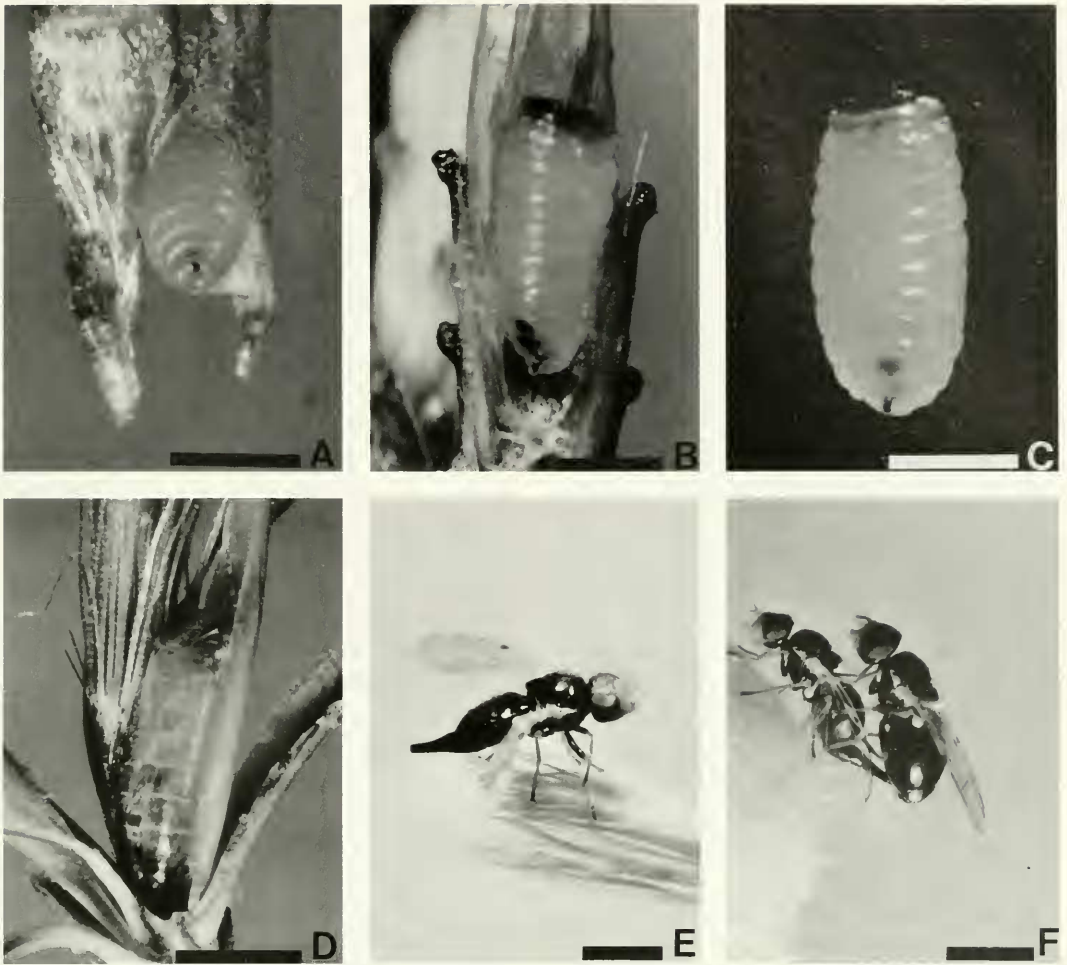after overwintering inside the dead flower

Fig. 4.   Life stages of *U. timberlakei*: (A) Second instar larva in attacked immature achenes of *Chrysothamnus viscidiflorus*; (B) third instar larva feeding in flower head of *C. teretifolius*; (C) nonfeeding, overwintering, prepupal, third instar dissected from flower head; (D) empty puparium in flower head of *C. viscidiflorus*; (E) female; (F) mating pair. Bars = 1 mm.

head. The larva reverses its orientation 180° and the puparium is formed with its anterior end facing outward, away from the receptacle (Fig. 4D). The adult emerges through the pappus bristles when exiting the puparium and flower head (Fig. 4D).

Adult.—The superficial resemblance of *U. timberlakei* adults to Agromyzidae in their lack of wing pattern and in their body size, pigmentation and pattern is noteworthy as possibly representing convergence or mimicry, but otherwise remains unexplained and unaddressed by the present study (Fig

4E, F). Males and females emerged together from mid-November to mid-January in the insectary from bulk samples of flower heads collected in mid-October, 1990 and 1991, that initially contained overwintering larvae. This emergence probably was abnormally early, as the spring hosts of *U. timberlakei* first bloom in April and May. All told, 23 ♂ and 22 ♀ and 20 ♂ and 10 ♀ were reared from these two samples, respectively. The most adults ever recovered by RDG from a single sample was 42 ♂ and 31 ♀ reared from a liter sample of heads of *C. viscidiflo-*

rus collected in Landers Meadow, Sequoia Nat. Forest, Kern Co., on 3.ix.1981. These and other published (Goeden 1987) and unpublished rearing records of RDG suggested a slightly male-biased sex ratio for *U. timberlakei*. Four of five females newly emerged from heads of *C. viscidiflorus* in the insectary contained two to <60, fully formed ova; the fifth female contained immature ovaries and considerable fat stored as 0.04-0.28-mm, irregular globules in the hemolymph. This suggested that the former females may have remained inside the flower heads, perhaps still inside their puparia, for undefined periods after they had molted and sexually matured and before they emerged. Like the early insectary emergence noted above, this suspected delay may have represented laboratory behavioral artifacts.

Wing displays.—Adults exhibited hamation as described for *N. viridescens* (Goeden and Headrick 1992). The wings in both sexes were held away from the body at ca. 45° without supination when at rest, then extended back and forth through 25–30° in a plane parallel to the substrate. Both sexes exhibited this display throughout the day concurrent with other behaviors, i.e. grooming, resting and feeding. Males also maintained hamation displays while facing a female for courtship.

Swaying.—Both sexes of *U. timberlakei* occasionally displayed swaying during hamation while facing another individual. Individuals swayed less during hamation when no other fly was nearby. Swaying during hamation sometimes preceded or followed side-stepping. Both sexes sidestepped during hamation while facing other individuals as described for *N. viridescens* (Goeden and Headrick 1992). The displaying adult moves sideways, up to one body length, in a semicircle and then back while facing the other individual. This movement continued for variable times and ended with one or the other fly decamping.

Courtship.—Male aggregative displays occurred throughout the day and lasted for several hours. Males typically held their

black abdomens slightly raised with the pleura fully distended. The abdominal pleura in *U. timberlakei* males undulated in waves of contraction that moved along the pleura from anterior to posterior. *U. timberlakei* males continued to hold their pleura distended throughout courtship and copulation, unlike other tephritid males that display abdominal pleural distension (cf., Headrick and Goeden 1990, 1991, 1993, Goeden and Headrick 1992, Headrick et al. 1993). Males occasionally interrupted their courtship displays to groom or feed. Males also commonly hung upside down in arenas visually following females while displaying hamation and abdominal pleural distension. Males displayed hamation and abdominal pleural distension during all hours of the day. Courtship was brief. Males approached females and abruptly jumped onto their dorsa with or without having exhibiting any prior wing displays toward them (n = 6). Females resisted males and jumped away from their mounting attempts. Males that were able to maintain their grip began copulatory induction behavior (n = 4).

Copulatory induction behavior (CIB).— Mounted males grasped females with the front legs gripping the dorsum of the abdomen near the thorax with the foreclaws hooked into the abdominal pleura. The middle legs wrapped around the base of the oviscape and the hind legs bent underneath the oviscape. Males used their hind legs to first raise the oviscape and place its apex against the epandrium. Generally, females strongly resisted males by using their hind legs to push at them. If males remained, the hind legs were rubbed vigorously against the sides and venter of the oviscape. When viewed from above, males shook rapidly from side-to-side through 30° over the female dorsum, as described for *N. viridescens* (Goeden and Headrick 1992).

Copulation.—The oviscape of *Urophora* females is relatively longer than that of most other species studied by us, except for *Procecidochares stonei* Blanc and Foote (Green et al. 1993). This caused some

unique problems for *U. timberlakei* males, as also observed with *P. stonei*. When receptive females exserted the aculeus and the male epandrium was not situated to receive its apex, the aculeus usually slid beneath the epandrium and posteriad of the male terminalia. This typically invoked vigorous CIB by males and repositioning of the terminalia. Males rocked back and forth over the female dorsum while the females continued to struggle. Males successful in engaging the aculeus tip were pushed farther backward as females exserted the ovipositor to its full length. The front legs of the male then grasped the base of the oviscape, the middle legs grasped the apex of the oviscape, and the hind tarsi were pressed against the fully exserted aculeus. This position was difficult for males to maintain and they struggled to move forward on the female by pressing the terminalia against the aculeus. Rhythmic retraction and exertion of the aculeus then began and continued until the final copulatory position was attained (Fig. 4F) (cf., Headrick and Goeden 1995). Two copulations were timed for their full duration and lasted 1 and 1.5 h.

Seasonal history.—*Urophora timberlakei* is at least bivoltine, probably trivoltine (see below), and synovigenic in southern California. Eleven males lived an average of 39 ± 5 days (range, 18–66 days); 14 females, 31 ± 6 days (range, 8–88 days) under insectary conditions. These mean longevities are longer than those of proovigenic females, e.g., *P. stonei* (Greene et al. 1993), but shorter than other synovigenic, univoltine females, e.g. *Paracantha gentilis* Hering (Headrick and Goeden 1990), or synovigenic, bivoltine females, e.g. *Tephritis arizonaensis* Quisenberry (Goeden et al. 1993). In southern California, the F_1 generation is produced in flower heads of spring-blooming hosts (*Acamptopappus* and *Amphipappus* spp., present study and Goeden 1987); the F_3 generation utilizes fall-blooming hosts (*Chrysothamnus* and *Haplopappus* spp., present study and Goeden 1987) and overwinters, as noted above,

as non-feeding third instars in dried, senescent flower heads. The summer is passed as F_1 adults, which we have observed to oviposit first on low-altitude populations of alternate hosts such as *C. viscidiflorus*, a widespread species which successively blooms from June through September at ever higher altitudes (RDG, unpub. data; Munz 1974). Thus, the F_2 and F_3 generations of *U. timberlakei* probably is produced on these long-blooming hosts at different elevations.

Natural enemies.—Only one parasitoid was reared specifically from *U. timberlakei* during this study, i.e. a single, solitary, endoparasitic female *Eupelmus* sp. (Hymenoptera: Eupelmidae) from one of four puparia dissected from a subsample of 400 flower heads of *C. viscidiflorus*. This subsample also yielded *Procecidochares minuta* (Snow).

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